EFFECTS OF THE NON-NATIVE GRASS, *PARAPHOLIS INCURVA* (POACEAE), ON THE RARE AND ENDANGERED HEMIPARASITE, *CORDYLANTHUS MARITIMUS* SUBSP. *MARITIMUS* (SCROPHULARIACEAE)

Meghan Q. N. Fellows

Natural Resource Management and Protection, Fairfax County Park Authority,
12055 Government Center Parkway, Suite 936, Fairfax, VA 22035
mnoefe@fairfaxcounty.gov

Joy B. Zedler

Department of Botany, University of Wisconsin, Madison, WI 53706

Abstract

We tested the host efficiency of an abundant non-native annual grass *Parapholis incurva* for the rare and endangered hemiparasite *Cordylanthus maritimus* subsp. *maritimus*. Flower production in *C. m. maritimus* was significantly less when *P. incurva* was the sole host (average 1 flower), than when the native perennial grass host, *Distichlis spicata*, was present (average 13 flowers). When *C. m. maritimus* was prevented from parasitizing either the native or non-native host, flower production results were similar to that of the non-native host (average 1 flower). Formation of haustoria did not differ between host identity treatments (average 270 haustoria per pot), but was significantly less in treatments that did not allow root contact between the host and hemiparasite (average 10 haustoria per pot). The "pseudo-host" effect of the non-native annual grass could result in high energetic cost to the endangered hemiparasite. Management decision-makers should factor in the costs of non-competitive mechanisms when prioritizing non-native species removal in areas with rare hemiparasites.

Key Words: non-native invasives, endangered, salt marsh, hemiparasite, haustoria.

If non-native species become abundant, they can significantly disrupt community structure and alter ecosystem function (Vitousek and Walker 1989; D'Antonio and Vitousek 1992; Fiedler and Ahouse 1992; Schmitz and Simberloff 1997; Wilcove et al. 1998). Three mechanisms by which non-native species affect ecosystems have been identified by Vitousek (1990), namely, resource sequestration, trophic alterations and disturbance-regime alterations (reviewed in D'Antonio and Vitousek 1992). However, with the exception of introduced top predators, species-specific effects of non-native on native species are infrequently documented, especially for plants (Lawler et al. 2002). Species that are rare as a result of habitat requirements, density constraints, or geographic limitation (Rabinowitz 1986; Fiedler and Ahouse 1992; Gaston 1994) may be especially susceptible to increased pressure from invasive species (Table 1). Endemic and parasitic plant species may be even more vulnerable, due to their very specific habitat requirements (Marvier and Smith 1997). California alone has more than 1500 endemic plant species (Raven and Axelrod 1978) and 165 parasitic plant species (Skinner and Pavlik 1994). The United States has 687 native parasitic plant taxa, of which 309 are considered rare on the state level (Kartesz 1999). One of these is the focus of our research.

We examined the novel plant-plant relationship of a non-native invasive grass, *Parapholis incurva* (L.) C.E. Hubbard, and a rare and federally endangered hemiparasite, *Cordylanthus maritimus* Nutt.

ex Benth. subsp. *maritimus*. Both are annuals that occur in close proximity in the high-intertidal habitats of southern California's coastal salt marshes. San Diego Bay, an international seaport with a Mediterranean-type climate, is especially susceptible to non-native species introductions. In its tidal marshes alone, 11 of 46 plant species are non-native (Sullivan and Noe 2000). In the 1996 and 1997 growing seasons, non-native species made up 36% and 40% of the seedlings, respectively, in the high-marsh habitat at Sweetwater Marsh National Wildlife Refuge (SWM) on San Diego Bay (Noe and Zedler 2001). The annual, *P. incurva*, dominated the seedling assemblage at SWM, comprising 26% and 18% of the total (Noe and Zedler 2001). At nearby Tijuana Estuary, *P. incurva* was the only non-native species that germinated in study plots, comprising 92% of seedlings in 1996 and 57% in 1997 (Noe and Zedler 2001). The abundance of non-natives in these marshes may increase as watersheds become increasingly urbanized and storm water runoff lowers the soil salinity and changes the structure and function of the downstream salt marsh (Kuhn and Zedler 1997; Callaway and Zedler 1998).

Rare marsh species may be negatively affected by the abundance of non-native plants. *Cordylanthus maritimus* subsp. *maritimus* has very limited geographic, habitat and community requirements that influence germination, establishment, survival and reproduction (Fig. 1) (Parsons and Zedler 1997; Fellows 1999; Noe and Zedler 2000). During 1996

TABLE 1. ATTRIBUTES OF *CORDYLANTHUS MARITIMUS* SUBSP. *MARITIMUS* THAT RELATE TO FIEDLER AND AHOUSE'S (1992) LIST OF CAUSES OF INTRINSIC RARITY. [1] Parsons and Zedler 1997, [2] Fink and Zedler 1989a, [3] Chuang and Heckard 1973, [4] Flick and Cayan 1985, [5] Helenurm and Parsons 1997, [6] PERL personal observation, [7] D. McIntire personal communication, [8] Mudie et al. 1976.

Causes of rarity	*Cordylanthus maritimus* subsp. *maritimus*
taxon ecology	restricted to upper tidal marsh[1]
life history strategy	non-host specific annual hemiparasite[2,3]
stochasticity	interannual fluctuations in rain, ENSO events[4]
reproductive biology	inefficient selfer, pollinator dependent[1]
taxon genetics	low variability[5]
population dynamics	colonies fluctuate in number and location[6]
coevolution	dependent predator, evidence for pollinator[1,7]
earth history	youngest salt marshes only 2000 years old[8]

and 1997, mean *C. m. maritimus* seedling abundance was only 3 and 2% of the all seedlings in the high-intertidal marsh at SWM and 7 and 9% at Tijuana Estuary (Noe and Zedler 2001). Historically, *C. m. maritimus* populations have fluctuated in response to changing environmental conditions. In a northern population of *C. m. maritimus* (Carpinteria Marsh), abundance ranged from one to over 10,000 individuals in a 27-year period (Chuang and Heckard 1973; W. Ferren, personal communication). An eight-year (1991–1998) monitoring effort at SWM recorded 10-fold variation in the abundance of a re-established population, as well as spatial shifts in its location (Zedler et al. 1995; Parsons and Zedler 1997; Zedler et al. personal observation). The fluctuations (from 14,000+ individuals to less than 1400 individuals) led us to question the population's sustainability and examine the factors that may influence its population dynamics. Non-native species have become more frequent in locations with *C. m. maritimus,* and although monitoring data do not allow us to draw conclusions about cause and effect, the observation is suggestive of a negative impact on the endangered species.
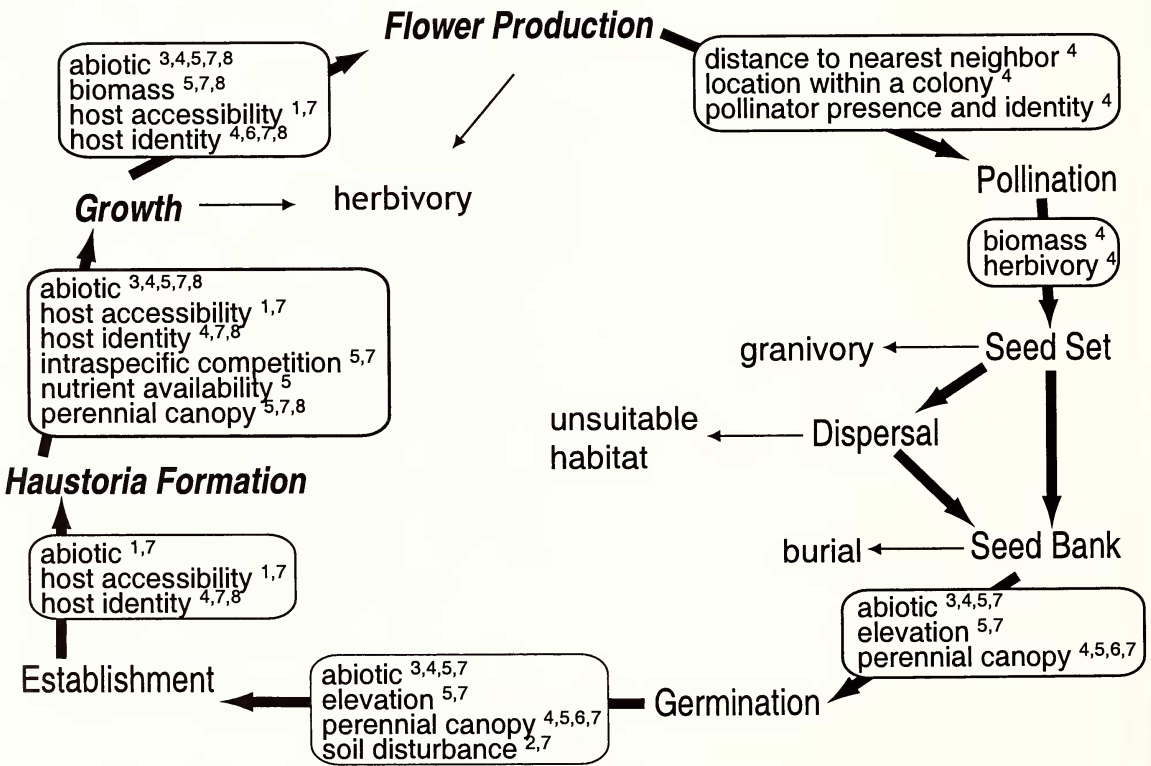

FIG. 1. Life processes of *Cordylanthus maritimus* subsp. *maritimus* and important and hypothesized important environmental factors. Non-native species are thought to influence processes indicated in bold and italics. [1]Chuang and Heckard 1971, [2]Cox and Zedler 1986, [3]Fink and Zedler 1989, [4]Fink and Zedler 1990, [5]Parsons and Zedler 1997, [6]Vanderwier and Newman 1984, [7]Fellows 1999, [8]this study.

Cordylanthus maritimus subsp. *maritimus* is a facultative hemiparasite (Chuang and Heckard 1971; Chuang and Heckard 1973; U.S. Fish and Wildlife Service 1984). Hemiparasitic plants, although able to photosynthesize, use haustoria (secondary roots) to attach to a host plant (Kuijt 1969). Haustoria generally function by providing water and/or nutrients to the hemiparasite (Piehl 1966; Kuijt 1969; Chuang and Heckard 1971); we know of no specific studies of haustoria function in *C. m. maritimus*. Haustoria in *C. m. maritimus* may be induced as early as the cotyledon stage, probably in response to physical cues in the environment (Chuang and Heckard 1971). Like most hemiparasites, *C. m. maritimus* growth is limited when none of its multiple host species is present (Fink and Zedler 1990). Almost all common tidal marsh plants within the elevation range of *C. m. maritimus* have been suggested as suitable host species, including perennial grasses (e.g., *Distichlis spicata* (L.) Greene, *Monanthochloe littoralis* Engelm.), perennial sub-shrubs (e.g., *Salicornia virginica* (L.)) and non-native annuals (e.g., *Polypogon monspeliensis* (L.) Desf.) (Vanderwier and Newman 1984; Fink and Zedler 1990). However, few studies have tested the mechanism for differential response of *Cordylanthus* species to its hosts (Fink and Zedler 1989; Marvier 1998). In the tidal marsh, the lifespan of most annuals, including non-native grasses like *P. incurva,* is out of synchrony with *C. m. maritimus.* While most annuals in the high-intertidal marsh senesce at the beginning of the dry season in early summer (May–June), *C. m. maritimus* initiates reproductive activity around May, peaking in July or August and may continue flowering until late September, suggesting annual species would probably not be suitable hosts. Host function during the hot and dry summer is critical for support of *C. m. maritimus*; therefore, the ability of a species to host *C. m. maritimus* needs to be tested under multiple seasonal conditions.

Cordylanthus maritimus subsp. *maritimus* has many natural constraints on its life cycle that contribute to its rarity (Fig. 1). The addition of a non-native species, such as *P. incurva,* could affect survivorship and reproduction of *C. m. maritimus.* The nature of this interaction is unknown. To assist managers in developing strategies for the recovery of *C. m. maritimus,* we explored the effects of different hosts under both wet and dry seasonal conditions.

METHODS

Biological Materials

Cordylanthus maritimus subsp. *maritimus* (*Cmm*) seeds were collected in 1995 from Tijuana River National Estuarine Research Reserve (U. S. Fish and Wildlife Service Collecting Permit #PRT 823806, Ca. 96-01-RP) and stored until December 1996 in a cool, dry environment. Seeds were cold treated at 4°C in January 1997 until November 1997 and then sowed directly into the experimental unit. Germination tests prior to the beginning of the experiment had 84% germination on wet filter paper (fresh water (0% salt)) in petri dishes in a growth chamber (13 h light: 11 h dark, 17°C).

In January 1997, cuttings of unknown aged *Distichlis spicata (Ds)* (a known host for *C. m. maritimus* (Fink and Zedler 1990)) were salvaged from a small area of Tijuana Estuary that was slated for excavation. *Distichlis spicata* is one of several hosts in southern California salt marshes and co-occurs with most *C. m. maritimus* populations. Cuttings were allowed to root in one of 18 propagation flats with well-watered, 2:1:1 perlite: vermiculite: top soil mixture with additions of vitamin B_{12} to encourage root growth. Cuttings that had rooted by June 1997 were transplanted into experimental pots by haphazardly selecting the pot and haphazardly selecting one cutting from a randomly chosen propagation flat. *Parapholis incurva (Pi)* is also present in most San Diego County salt marshes, co-occuring with *C. m. maritimus, Distichlis spicata* and other *C. m. maritimus* hosts. Seeds were collected in 1997 from two areas of Tijuana Estuary. Seeds were stored at 4°C for 6 months, soaked for 24 hours in water purified by reverse osmosis and then sowed directly into the experimental unit in July 1997.

Experimental Approach

The effect of *P. incurva* on *C. m. maritimus* was tested in an outdoor pot experiment at San Diego State University, using a complete two × three factorial design with two levels of water availability and three host treatments (*Pi, Ds,* and *Pi+Ds*), with five replicates per treatment (Fig. 2). Salinity was not included as a factor because none of the taxa are obligate halophytes and constant soil salinities are notoriously difficult to control in greenhouse conditions. Water baths maintained either 'watered' (water level at or near top of bath) or 'drought' (water drained from bath, until dry) treatment conditions. Each bath held one replicate of each host treatment. Because of the much smaller biomass of the non-native grass, we attempted to constrain initial host stem number to be constant across treatments, regardless of plant number. This resulted in host densities consisting of two to four plants of *P. incurva* (*Pi*), one plant (one or two root nodes) of native *D. spicata* (*Ds*), and up to five plants in *Pi+Ds*, maintaining the same density as when grown alone (i.e., *Pi+Ds* treatments had twice the number of stems). Each pot also contained one *C. m. maritimus* that had been haphazardly thinned from seedlings that germinated from directly sown seed.

A second experiment, run concurrently, tested the belowground effects of the hosts and the hemiparasite. The complete two × three factorial design had two water availability levels and three host accessibility treatments (*Cmm* alone (i.e., no host),
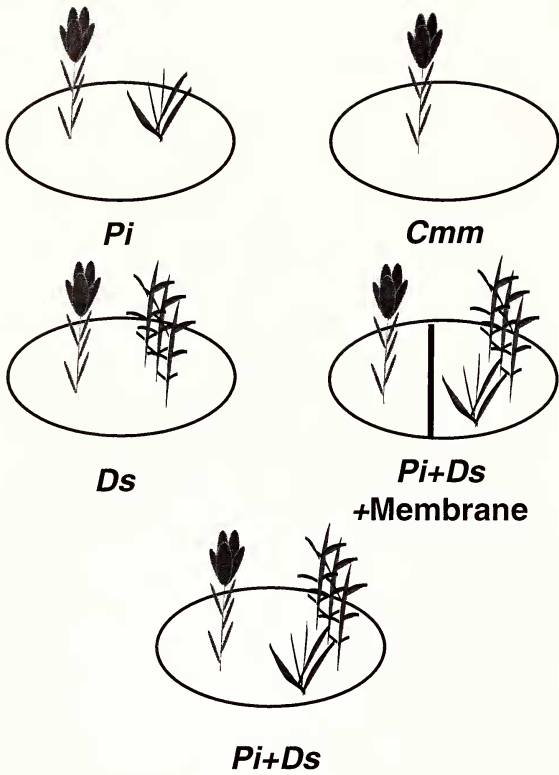
FIG. 2. Experimental design for host interaction tests. Treatments included *Parapholis incurva* (*Pi* only), *Distichlis spicata* (*Ds* only) or both (*Pi+Ds*) and *Cordylanthus maritimus* ssp. *maritimus* (*Cmm* only), both hosts separated by a membrane (*Pi+Ds*+Membrane) or both hosts (*Pi+Ds*).

Pi+Ds+Membrane (i.e., no root connection), and *Pi+Ds*) (Fig. 2). Water baths maintained treatment conditions as above. In pots with hosts and *Cmm*, the same number of stems was maintained in this experiment as the first experiment. A 30-μm mesh membrane was buried in pots of *Pi+Ds*+ Membrane that allowed water and nutrient movement but no haustorial connection between *C. m. maritimus* and its potential hosts.

For both experiments, the experimental unit was a tall pot made out of a 90-cm section of drain pipe (8-cm diameter), sealed at the bottom with felt, filled with sand to within 5-cm of the top, and planted with the appropriate host propagules and a *C. m. maritimus* seedling. Pots were kept upright in a frame under a clear plastic canopy to exclude rain. As there were no obvious environmental differences within the 0.6 × 3.2-m experimental site, the units were kept in their original random locations. The experiments ran for eight months, from November 1997 to June 1998.

Pots were monitored twice a month until *C. m. maritimus* appeared to have reached maximum flowering, a minimal number of plants had senesced, and a natural eight-month, lifespan had transpired. The two hosts were in variable condition with most of the annual host, *P. incurva*, recently senescent while the perennial host, *D. spicata*, appeared healthy. Flower number and haustoria number of *C. m. maritimus* were counted once, at the termination of the experiment. Root material was separated from the sand by spraying water over a 0.03-mm mesh screen. Roots of both host and hemiparasite were hydrated and examined for haustoria visible to the unaided eye (typical haustoria are 2 mm in diameter). Seed number was not monitored because suitable pollinators were not expected to be present at the location of the experiment, therefore seed production would be artificially low (Parsons and Zedler 1997). Organic material was separated by species for aboveground and, when possible, belowground biomass. Biomass of each component was dried at 60°C until constant weight and measured.

A two-way analysis of variance was used to test the significance of water level and host identity (or host accessibility) as main, categorical effects (SYSTAT 1992). Flower and haustoria number were log-transformed to improve the fit of the data to the assumptions of the analysis of variance. Multiple comparisons of flower and biomass data were performed with Tukey's post-hoc test (SYSTAT 1992). Survival data could not be statistically analyzed because categorical counts were less than five, and in some cases zero (SPSS 1999, Multinomial Logit Model; Ott 1992).

RESULTS

The non-native annual *Parapholis incurva* supported less flower production in the hemiparasite than the native perennial *Distichlis spicata* (Fig. 3A). *Cordylanthus maritimus* subsp. *maritimus* grown with *D. spicata* had twelve times as many flowers than when grown with *P. incurva* (Tukey's HSD *Pi* vs. *Ds* P = 0.020, *Pi* vs. *Pi+Ds* P = 0.042; F = 11.492, P ≤ 0.001) (Fig. 3A). Haustoria number (F = 0.591, P = 0.562) did not show a significant effect of host species identity, but there was much variability (Fig. 3B). Survival data are presented but not statistically analyzed (Fig. 3C). Significance of results did not differ when calculated per experimental unit or per surviving *C. m. maritimus* individual. There was a strong correlation between *C. m. maritimus* flower number and dry-weight biomass (r = 0.834, P ≤ 0.001).

Water treatment did not affect *C. m. maritimus* flower number; watered plants averaged 10.0 ± 2.8 flowers (mean ± 1 SE), while those undergoing drought averaged 9.1 ± 2.8 flowers (F = 0.003, P = 0.96) (Fig. 3A). Drought treatment may have stimulated haustoria production (Fig. 3B), as watered pots had a mean of 131.9 ± 27.8 haustoria per pot as compared to 269.2 ± 59.5 for drought-treated pots (F = 3.336, P = 0.080). There was no interaction between water treatment and host treatment for either flower or haustoria number.
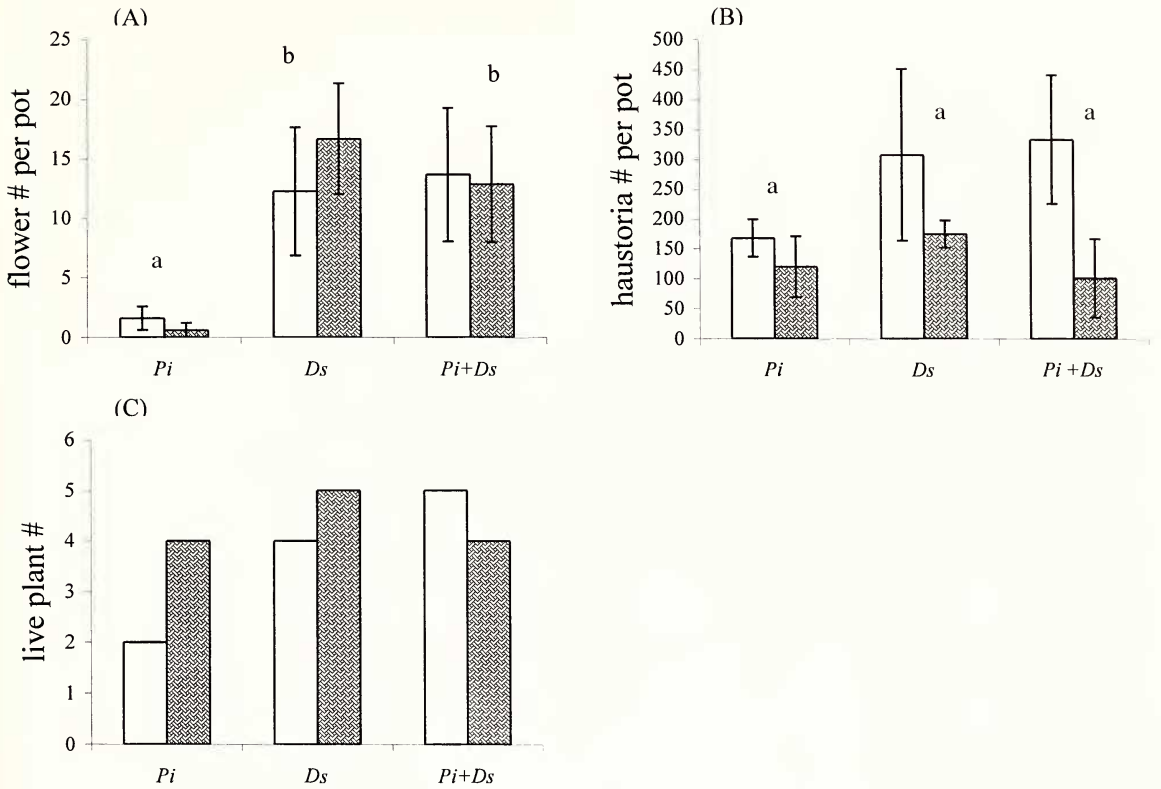
FIG. 3.   Responses of *Cordylanthus maritimus* subsp. *maritimus* to three host identity treatments. A. Number of flowers per pot; B. Number of haustoria per pot; C. Survival through the eight-month experiment (n = 5, with one plant/pot; not analyzed statistically due to low n). Small letters signify differences (p ≤ 0.001); error bars are ±1 SE. Open bars are treatments with simulated drought. Abbreviations are defined in Figure 2 caption.

Biomass in pots with *D. spicata* was greater than in pots with the non-native *P. incurva* alone. *Parapholis incurva* in pots with both hosts had half as much aboveground biomass (*Pi+Ds*: 0.25 ± 0.03 g per pot) as when grown alone (*Pi*: 0.56 ± 0.07 g per pot) (F = 40.116, P ≤ 0.001). *Distichlis spicata* biomass was unaffected by *P. incurva* presence (*Pi+Ds*: 0.74 ± 0.12 g per pot vs. Ds: 0.83 ± 0.09 g per pot; Tukey's HSD P = 0.758). Below-ground biomass was also much greater in treatments that included *D. spicata* (*Pi*: 0.303 ± 0.04, *Ds*: 2.196 ± 0.24, *Pi+Ds*: 2.555 ± 0.54 (all g per pot); Tukey HSD *Pi* vs. *Ds*: P = 0.002 and *Pi* vs. *Pi+Ds*: P ≤ 0.001). Water treatment did not affect the biomass of the host shoots (*Ds*: F = 2.53, P = 0.124, *Pi*: F = 1.37, P = 0.25) or roots (F = 1.119, P = 0.300).

Restricting accessibility of host roots to *C. m. maritimus* with a fine pore membrane negatively affected *C. m. maritimus* flower number. Flower production averaged 17.5 ± 5.4 in *Pi+Ds* pots but only 1.0 ± 0.7 flower in *Cmm* or *Pi+Ds+*Membrane pots (Fig. 4A) (log transformed, F = 15.33, P ≤ 0.001). Pots had 20 times as many haustoria in the *Pi+Ds* treatment than in either *Cmm* alone (Tukey's HSD P ≤ 0.001) or *Pi+Ds+*Membrane (Tukey's HSD P = 0.003) (F = 43.22,

P ≤ 0.001) (Fig. 4B). Survival of *C. m. maritimus* was very low in the *Pi+Ds+*Membrane treatment, with just two of the original 10 plants alive at experiment termination (Fig. 4C).

As in the first experiment, flower number was unaffected by water treatment (F = 0.06, P = 0.81) (Fig. 4A) and there was no water and host accessibility interaction (F = 0.21, P = 0.810). Again, haustoria production was unaffected by watering (F = 0.38, P = 0.54), although there was a significant interaction with host accessibility (F = 3.02, P = 0.07) (Fig. 4B).

Host aboveground biomass was greater in pots with a host present, of course, but unaffected by exclusion of root contact with the hemiparasite (F = 24.794, P ≤ 0.001; *Pi+Ds+*Membrane: 0.59 ± 0.05 g per pot, *Pi+Ds*: 0.90 ± 0.15 g per pot, Tukey's HSD P = 0.149) or by water availability (watered: 0.55 ± 0.04 g per pot, drought: 0.41 ± 0.10 g per pot; F = 0.67, P = 0.43). Root biomass was greater in all pots with host roots (F = 35.42, P ≤ 0.001; *Cmm* alone: 0.005 ± 0.001 g per pot, *Pi+Ds+*Membrane: 1.069 ± 0.166 g per pot, *Pi+Ds*: 2.138 ± 0.252 g per pot) although greater when roots were not excluded (Tukey's HSD *Pi+Ds+*Membrane vs. *Pi+Ds*, P = 0.006).
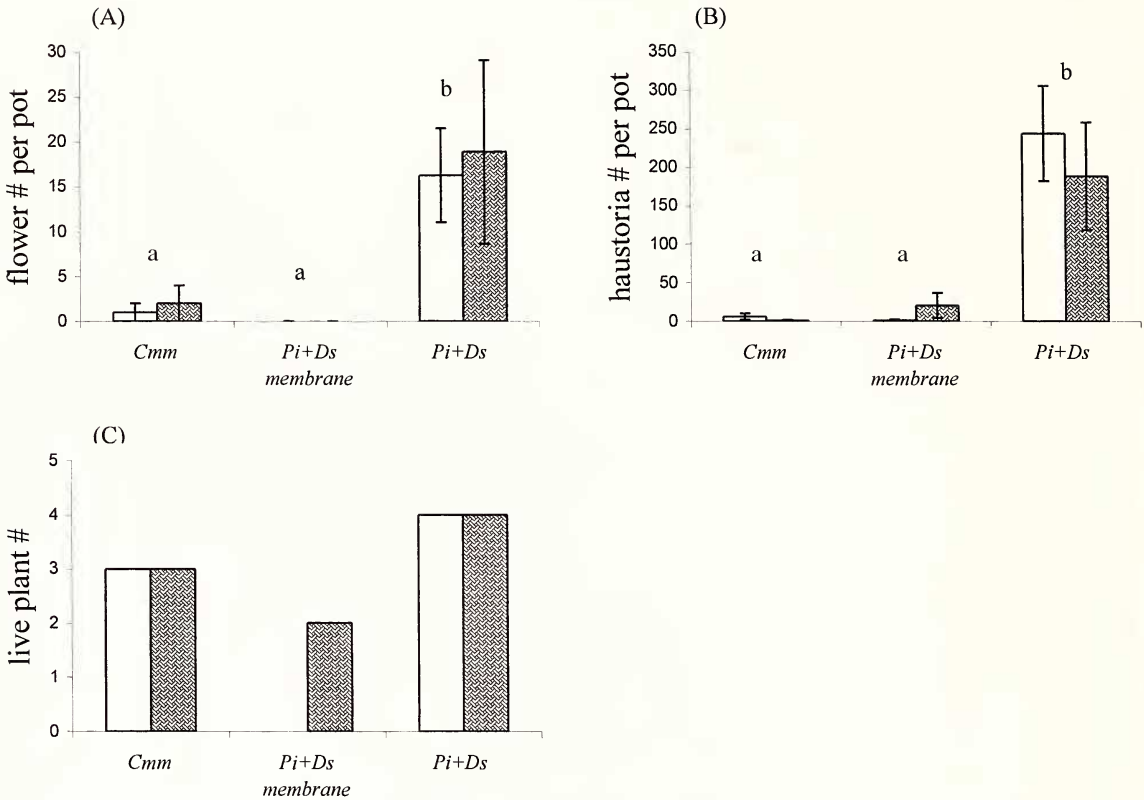
FIG. 4. Responses of *Cordylanthus maritimus* subsp. *maritimus* to three host availability treatments. A. Number of flowers per pot; B. Number of haustoria per pot; C. Survival through the eight-month experiment (n = 5, with one plant/pot; not analyzed statistically due to low n). Small letters signify differences (p ≤ 0.001); error bars are ±1 SE. Open bars are treatments with simulated drought. Abbreviations are defined in Figure 2 caption.

DISCUSSION

Effects of a Non-Native, Annual Host

The plant host-hemiparasite interaction may be affected by a multitude of factors, including: host health (Salonen and Puustinen 1996), abiotic stress (e.g., salinity, soil moisture, soil quality), hemiparasite density (parasite depression), and host density (intraspecific competition). Parasites show host preference by development of a cue/response system (i.e., chemical or physical); even "host generalists" exhibit a range of host preference (Kuijt 1969; Calladine et al. 2000) suggesting that not all hosts are equal. In this experiment, drought, lack of nutrient additions and high plant density all contributed to stressful conditions, so issues of comparative host health are not likely to be confounding in this study. Nutrient poor conditions are also typical of southern California salt marshes (Zedler et al. 1992), and were not seen as a significant stress on the experimental plants. Thus, we attribute results to the treatments, which included alternative hosts and limited host accessibility.

We showed that the endangered hemiparasite, *Cordylanthus maritimus* subsp. *maritimus* produced far fewer flowers when grown with the non-native annual grass *Parapholis incurva* than with the native perennial host *Distichlis spicata* (Fig. 3A). Also, *C. m. maritimus* flower production was substantially reduced when a belowground host was unavailable (Fig. 4A). Haustoria production (as measured as final haustoria count), however, was similar when either host's roots were available, even though nearly no haustoria were produced when *C. m. maritimus* was grown alone.

Although we could not statistically test whether the non-native *P. incurva* host led to a premature death of *C. m. maritimus* individuals, the reduced flower production alone could decrease long-term sustainability of *C. m. maritimus* populations by depressing seed production. Further reducing reproductive potential, the abundance of *P. incurva* (e.g., the 91.5% of seedlings in *C. m. maritimus* habitat at Tijuana Estuary in 1996 (Noe and Zedler 2001)) could reduce *C. m. maritimus* population viability by decreasing the number of pollinator visits due to the smaller visual cue of a smaller number of flowers (Parsons and Zedler 1997). Reduced flower production defines a specific mechanism by which a non-native plant could decrease native plant function and sustainability in the natural ecosystem.

Haustoria Function

Haustoria function is rarely quantified (exceptions include Marvier 1998 and Calladine et al. 2000). One elegant technique to determine function is to measure the secondary compounds that may flow through the haustoria connection (e.g., Marvier 1998). More often, function is assumed if haustoria are observed to penetrate the host root (e.g., Calladine et al. 2000). Haustoria counts on 20 different potential native hosts of *Nuytsia floribunda* (Labill.) R.Br. did not strongly correlate with hemiparasite biomass, leading to the suggestion of a gradient of function based on species-specific anatomy or proportional exchange of organic solutes (Calladine et al. 2000). Although *P. incurva* might have affected the hemiparasite *C. m. maritimus* by preventing haustoria production, allowing the formation of anatomically non-functional haustoria or depressing the effect of properly functioning haustoria (either through the shorter-lived *P. incurva* senescence or a physiologic mechanism), we found no evidence of the first mechanism. A detailed anatomical study to determine if the visible haustoria were indeed penetrating the host roots and fully functional was beyond the scope of this ecologically-focused study. However, we do know that in both drought and well-watered conditions, the number of haustoria did not differ between host treatments (Fig. 3B). Hence, we attribute the reduced reproductive potential of *C. m. maritimus* to some level of reduced haustoria function, whether it is an anatomic failure, or merely a failure of the annual *P. incurva* to provide the necessary compounds to *C. m. maritimus.*

Production of functional haustoria can benefit the hemiparasite by increasing the amount of water and/or nutrients available to the plant. The trend of increased haustoria production observed in the drought treatments suggests that *C. m. maritimus* can respond to changing environmental conditions. Alternatively, the cost of a non-functioning haustorium, or one that operates at a reduced function, may be detrimental to the hemiparasite. Shedding of non-functional function-specific roots, is not unknown in the plant kingdom, e.g., rain induced roots (Hunt et al. 1987) or in response to lack of soil N (Burton et al. 2000). Although survivorship data could not be statistically analyzed, some mortality of *C. m. maritimus* individuals in the *Pi* treatment (Fig. 3C) could be one negative outcome of unsuccessful parasitism. A future study to determine the cost of producing non-functioning haustoria could define the potential negative impact of non-functional haustoria on growth and reproduction of *C. m. maritimus.*

Management Implications

A basic understanding of the ecology of rare species (Fig. 1) is needed before populations can be conserved, recovered, reintroduced, or introduced. This is especially important when the ecosystem is being created from a different system or new land (e.g., wetlands from dredge spoils). Non-native species invasions are known to slow ecosystem restoration efforts (Callaway and Sullivan 2000). Others have focused on non-native species' effects on resources (e.g., sequestration of water or nutrients), altered trophic interactions (e.g., carnivory, herbivory, granivory) and alterations of disturbance regimes (e.g., fire frequency; reviewed by Vitousek 1990). To this list we add interference with parasite-host efficiency. For the over 3000 parasitic angiosperm species that depend on specific host attributes (Marvier and Smith 1997), non-native species may cause an additional hurdle by interrupting host plant-parasite interactions. A parasite that attaches to a host that cannot support it to the reproductive stage experiences direct interference. In effect, the non-native species is a "pseudo-host," allowing haustoria formation, but not necessarily contributing to the maintenance of the hemiparasite. The removal of abundant non-native species, and establishment of native host species would appear to be desirable for improving growth and flowering (and thus reproduction) of *C. m. maritimus.*

Non-native species are recognized as a primary cause of species endangerment, second only to habitat destruction (Schmitz and Simberloff 1997; Wilcove et al. 1998). Hence, managers need to create high quality habitats, free of non-native species. While management plans often call for the removal of invasive species for reasons of aesthetics, fire control, improved water management, or replacement of monocultures to increase biodiversity, our results suggest another subtle benefit, namely increased reproduction of rare parasitic plants.

Literature Cited

Burton, A. J., K. S. Pregitzer, and R. L. Hendrick. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia 125:389–399.

Callaway, J. C. and G. Sullivan. 2000. Sustaining restored wetlands: identifying and solving management problems. Pp. 337–362 *in* J. B. Zedler (ed.), Handbook for restoring tidal wetlands. CRC Press, Boca Raton, FL.

——— and J. B. Zedler. 1998. Interactions between a salt marsh native perennial (*Salicornia virginica*) and an exotic annual (*Polypogon monspeliensis*) under varied salinity and hydroperiod. Wetlands Ecology and Management 5:179–194.

Calladine, A., J. S. Pate, and K. W. Dixon. 2000. Haustorial development and growth benefit to seedlings of

the root hemiparasitic tree *Nuytsia floribunda* (Labill.) R.Br. in association with various hosts. Annals of Botany 85:733–740.

CHUANG, T. I. AND L. R. HECKARD. 1971. Observations on root-parasitism in *Cordylanthus maritimus* (Scrophulariaceae). American Journal of Botany 58:218–228.

——— AND L. R. ———. 1973. Taxonomy of *Cordylanthus maritimus* subgenus Hemistegia (Scrophulariaceae). Brittonia 25:135–158.

D'ANTONIO, C. M. AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

FELLOWS, M. Q. 1999. Recovering a rare and endangered hemiparasite: interactions and effects of native and exotic hosts. M.S. thesis. San Diego State University, San Diego, CA.

FIEDLER, P. L. AND J. J. AHOUSE. 1992. Hierarchies of cause: toward an understanding of rarity in vascular plant species. Pp. 23–47 *in* P. L. Fiedler and S. K. Jain (eds.), Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York, NY.

FINK, B. AND J. B. ZEDLER. 1989. Maximizing growth of *Cordylanthus maritimus* subsp. *maritimus,* an endangered salt marsh plant. Progress Report to California Department of Transportation. Pacific Estuarine Research Laboratory, San Diego State University, San Diego, CA.

——— AND J. B. ZEDLER. 1990. Endangered plant recovery: experimental approaches with *Cordylanthus maritimus* subsp. *maritimus.* Pp. 460–468 *in* H. G. Hughes and T. M. Bonnicksen (eds.), Proceedings of the First Annual Meeting of the Society for Ecological Restoration. Society for Ecological Restoration, Madison, WI.

GASTON, K. J. 1994. Rarity. Chapman and Hall, New York, NY.

HUNT, E. R. JR., N. J. D. ZAKIR, AND P. S. NOBEL. 1987. Water costs and water revenues for established and rain-induced roots of *Agave deserti.* Functional Ecology 1:125–129.

KARTESZ, J. T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland, 1st ed. *In* Kartesz, J. T. and C. A. Meacham. Synthesis of the North American Flora, Version 1.0. North Carolina Botanical Garden, Chapel Hill, NC.

KUHN, N. L. AND J. B. ZEDLER. 1997. Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. Estuaries 20:391–403.

KUIJT, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley, CA.

LAWLER, J. J., S. P. CAMPBELL, A. D. GUERRY, M. KOLOZSVARY, R. J. O'CONNOR, AND L. C. N. SEWARD. 2002. The scope and treatment of threats in endangered species recovery plans. Ecological Applications 12:663–667.

MARVIER, M. 1998. A mixed diet improves performance and herbivore resistance of a parasitic plant. Ecology 79:1272–1280.

MARVIER, M. A. AND D. L. SMITH. 1997. Conservation implications of host use for rare parasitic plants. Conservation Biology 11:839–848.

NOE, G. B. AND J. B. ZEDLER. 2000. Differential effects of four abiotic factors on the germination of salt marsh annuals. American Journal of Botany 87: 1679–1692.

——— AND ———. 2001. Spatiotemporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. Journal of Vegetation Science 12:61–74.

OTT, R. L. 1992. An introduction to statistical methods and data analysis. Duxbury Press, Belmont, CA.

PARSONS, L. S. AND J. B. ZEDLER. 1997. Factors affecting reestablishment of an endangered annual plant at a California salt marsh. Ecological Applications 7:253–267.

PIEHL, M. A. 1966. The root parasitism of *Cordylanthus maritimus* and some of its ecological implications (abstract). American Journal of Botany 53:622.

RABINOWITZ, D., S. CAIRNS, AND T. DILLON. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182–204 *in* M. E. Soulé (ed.), Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.

RAVEN, P. H. AND D. I. AXELROD. 1978. Origin and relationships of the California flora. University of California Publications in Botany 72. University of California Press, Berkeley, CA.

SALONEN, V. AND S. PUUSTINEN. 1996. Success of a root hemiparasitic plant is influenced by soil quality and by defoliation of its host. Ecology 77:1290–1293.

SCHMITZ, D. C. AND D. SIMBERLOFF. 1997. Biological invasions: a growing threat. Issues in Science & Technology 13:33–40.

SKINNER, M. W. AND B. M. PAVLIK. 1994. California Native Plant Society's inventory of rare and endangered plants of California, 5th ed. California Native Plant Society, Sacramento, CA.

SPSS. 1999. SPSS 10.0 for Windows, Advanced Modules. SPSS, Inc., Chicago, IL.

SULLIVAN, G. AND G. B. NOE. 2000. Appendix 2: coastal wetland plant species of southern California. Pp. 369–394 *in* J. B. Zedler (ed.), Handbook for restoring tidal wetlands. CRC Press, Boca Raton, FL.

SYSTAT. 1992. SYSTAT Version 5.2.1 for the Macintosh. SYSTAT, Inc., Evanston, IL.

U.S. FISH AND WILDLIFE SERVICE. 1984. Recovery plan for salt marsh bird's beak (*Cordylanthus maritimus* subsp. *maritimus*). U.S. Fish and Wildlife Service, Portland, OR.

VANDERWIER, J. M. AND J. C. NEWMAN. 1984. Observations of haustoria and host preference in *Cordylanthus* subsp. *maritimus* at Mugu Lagoon. Madroño 31:185–186.

VITOUSEK, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13.

——— AND L. R. WALKER. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59:247–265.

WILCOVE, D. S., D. ROTHSTEIN, J. DUBOW, A. PHILLIPS, AND E. LOSOS. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

ZEDLER, J. B., C. S. NORDBY, AND B. E. KUS. 1992. The ecology of Tijuana Estuary. A National Estuarine Research Reserve. Pacific Estuarine Research Laboratory, San Diego State University, San Diego, CA.

———, K. BOYER, J. HALTINER, G. NOE, L. PARSONS, S. PHINN, D. STOW, AND G. WILLIAMS. 1995. The status of constructed wetlands at Sweetwater Marsh National Wildlife Refuge. Annual Report to the California Department of Transportation. Pacific Estuarine Research Laboratory, San Diego State University, San Diego, CA.